

THE ANNALS

AND

MAGAZINE OF NATURAL HISTORY.

[THIRD SERIES.]

No. 110. FEBRUARY 1867.

XVI.—*On the Fecundation of the Fungi.* By H. KARSTEN*.

My observations on the development of the apothecium of *Cænogonium*† led me at once to the probable supposition of an analogous process in the formation of the fruit in the Fungi. I saw the fruit of a Lichen, the apothecium of *Cænogonium*, with all its spore-sacs and paraphyses, forming an hymenial stratum, develope itself from a single cell equivalent to a gonidial cell, and, indeed, after a previous coalescence, and apparently after the mingling of its contents with those of a branch of the cortical cells closely applied to its surface, which is furnished with porously thinned spots.

The question immediately arose whether the partly very similarly constructed fruit of the Discomycetes, as well as of the other allied tubular Fungi, and even those of the Hymenomycetes, were not produced in consequence of a similar process of copulation‡. The confirmation of this idea would lead to simple laws as to the multiplication of plants, expressible in the following manner:—

1. The typical form of every true species of plants is propagated and maintained by sexually produced germs.

2. Whilst the fecundated germ-cell is developed, in the Phanerogamia, into a single germ which usually rests in its envelopes for a longer or shorter period, and in the vascular Cryptogamia into one which evolves itself at once, in the cellular Cryptogamia it is developed generally into a composite fruit containing numerous seeds§.

* Translated by W. S. Dallas, F. L. S., from 'Botanische Untersuchungen,' 1866, pp. 160–169.

† Das Geschlechtsleben der Pflanzen und die Parthenogenesis, 1860, and Gesammelte Beiträge, p. 317. [Annals, 3 ser. vol. viii. p. 203.]

‡ Gesammelte Beiträge, p. 341.

§ Das Geschlechtsleben der Pflanzen und die Parthenogenesis. Ges. Beitr. p. 340.

The supposition that the mode of development ascertained, indeed, only from this single example occurs also in the other composite fruits of the Lichens and Fungi, is supported by the analogous development of the fruits of the leafy cellular Cryptogamia.

In Mosses and Liverworts the germ-cell contained in the archegonium, after fecundation by means of antherozoids in the same way as in vascular Cryptogamia, multiplies into a great number of seeds and at the same time becomes developed into an envelope for these, constructed with so many modifications that until recently it could be almost exclusively employed for the classification of these plants. In like manner, if the result obtained in the case of *Cænogonium* be found to apply also to the other Lichens and Fungi, the fertilized germ-cell of these also grows into a fruit of complicated structure, usually serving as an envelope to innumerable seeds, and here also presenting itself in such multifarious forms that it has likewise been employed in systematic botany for the arrangement of the Fungi in genera and families.

Between the two great divisions of the Cryptogamia established in accordance with their histological structure and the formation of their fruits, the vascular and cellular Cryptogamia, the Algæ, hitherto likewise but imperfectly known as regards the development of their fruit, would apparently take their place.

In order to test these ideas, as soon as I had completed the investigation of *Cænogonium*, I undertook the dissection and observation of the developmental history of the fruits of Fungi, although in their earliest stages these organs (which, from their great delicacy, elude dissection, and by the inclusion of air in all the larger interstices of their loose tissue become opaque) present to the anatomist even greater difficulties than the fruit of the lichens, which from their smallness alone are so difficult to dissect that several recent authors have been unsuccessful in performing this operation.

In *Agaricus campestris*, Linn., by gradually going back from the forms recognizable with certainty as the youngest states of the cap to smaller ones, I found an organ which, from its peculiar form and texture, I could not but regard as the first commencement of the fruit. This was an oval, almost egg-shaped simple cell, standing upon a short peduncle of the thickness of the mycelium, and of from three to four times the diameter of this, filled with albuminous matter and overgrown by filaments of the mycelium, which were at first single, but by continually increasing in number, at last form a thick rind (peridium, velum)

over the central ovicell, which in the meantime increases in size*.

A similar organ, according to Bary, was lately found by Oerstedt on the mycelium of another species of this genus, namely, *A. variabilis*. This accomplished observer also mentions elongate, reniform, pedunculated cells, containing albuminoid plasma and apparently a nucleus. Near these cells, regarded as equivalent to the female organs, Oerstedt found filamentous organs, the ends of which were generally turned away from these cells, and rarely bent towards them: these appeared to Oerstedt to have possibly the function of anthers. Without any further perceptible changes, the ovicell is afterwards enveloped by a web of mycelium-filaments, which spring from the branch bearing it; by this means the foundation of the cap is laid.

This result harmonizes to a certain extent with my above-mentioned view attained by the observation of the development of the fruit of *Cænogonium*, and corresponds both with my above-detailed observations on *A. campestris* and with those which I have since had the opportunity of making upon *A. vaginatus*, Bull. The latter, indeed, only enable us to advance one step in the elucidation of this difficult subject; but as we are so completely unacquainted with the first stages of development of the fruit of Fungi, they may nevertheless fitly be communicated here, in order to incite to a further investigation of the subject.

For the repetition of these observations I selected *A. vaginatus*, because, from its smooth mycelium-filaments, it seemed to me to be better suited to the purpose than *A. campestris*.

By going back from the developed fruits to younger states, on the mycelium of this Agaric also I found, as the first indication and commencement of the pileus, simple cells of oblong form, at first with short but afterwards with longer foot-stalks, from two to five times the breadth of the filaments of the mycelium. These had turbid albuminous contents (not shining, as in *A. campestris*); and in their centre a nuclear cell, filled with rather clearer fluid, could be recognized. The pedicels were separated by a septum both from the dilated terminal cell and from the filament of the mycelium. Once I found two such cells close together, both, however, with rather short pedicels, and without any other branches in their vicinity (fig. 1). That these bodies are not parasitic structures, but organs of the fungus itself, is shown by the continuity of these branches, and their perfect similarity in structure with those of the mycelium-filament, beset with the commencements of fruit in their immediate vicinity, from which they originated; that they cannot be

regarded as gonidia or so-called spermatia, but are the first commencement of the fruit of the Fungus, is also proved by their subsequent stages of development.

Thus similar oval cells, but with rather longer pedicels, had beside them a cylindrical cell likewise springing from the mycelium, and only slightly exceeding its filament in thickness. I suppose that such cylindrical cells would also have sprouted forth near each of the two cells figured (fig. 1) when these had become a little older. But I once found this cylindrical filament, which consists of two cells, and slightly exceeds the oval terminal cell of the filament first produced, closely applied to the latter, and containing a turbid fluid in its superior cell (fig. 2). The oval cell was then not filled with such uniform contents as in its younger states, but with a vesicular frothy matter, which had drawn together towards the side of the cell which was in contact with the neighbouring filament, so that in this cell, on the side opposite to the latter filament, there was a space free from the albuminous contents and filled only with watery fluid.

The most remarkable thing about this object seemed to me to be the circumstance that the oval terminal cell of the first-formed branch appeared at its point of contact with the cylindrical terminal cell of the later-formed branch to be, as it were, pressed into the latter, and even when moved and pulled, by which means the apex of the filiform branch was torn away, it did not separate therefrom, and was apparently amalgamated with it at this point of contact. Such an amalgamation of two neighbouring mycelium-filaments is very unusual in this fungus; and we must therefore suppose that these two amalgamated branches had some extraordinary relations to each other.

Moreover this spot where the amalgamation took place possessed a structure different from that of the rest of the walls of these two branches. For while in other parts the membranes of these two branch-cells presented no difference from those of the mycelium-filaments (unless, perhaps, the wall of the oval cell might be rather more delicate), this point of contact and amalgamation was rather more thick-walled, more turbid, rough, and, so far as could be judged from the position, which was not very favourable for examination, was somewhat similar to the finely porous perforated walls.

The turbid, granular contents which flowed out on the rupture of the terminal cell of this branch, and mixed with the water in which the object lay, showed small elongated cellulules filled with clear contents: these, as it appeared to me, are the small dark corpuscles like granules of cell-contents, which by endosmosis of the water in which they floated became so far

expanded, and thus could be more clearly recognized than when imbedded in the turbid cell-juice within their mother cell.

From the lower parts of both branches, that bearing the cylindrical, as well as that bearing the oval terminal cell, small ramifications had sprouted (fig. 2). Similar ramifications occurred on others in greater quantity. They curved over the oval terminal cell (which had in the meanwhile grown larger), and removed this entirely from observation, not only by their own presence, but especially by their speedily collecting between them a quantity of air insoluble in water.

But in this stage of development these two cells were not always so distinctly perceptible by their uncovered inferior extremity as in the case represented in fig. 3: the rudiment of the fruit, when it had attained this small size and acquired a more or less globular form, was usually seated immediately upon the mycelium-filament.

Sometimes I detected among these mycelium-filaments, after the removal of the air by the air-pump, the vertex of a simple thin-walled cell, of about twice the size of the free oval branch-cell. Twice I succeeded in isolating the cell partially from the filaments enveloping it—that is to say, in separating the upper part, embracing two-thirds of the entire cell, from the latter; the inferior third was always so amalgamated with the filaments, which here lie closer together, that it remained united therewith (fig. 4). The very delicate membrane was somewhat folded and rumpled; cellular contents could be detected in neither case, but only a covering of the inner surface with an irregularly distributed yellowish plasma. It could not be decided whether this coating of the wall indicated the previous presence of delicate endogenous cells, which might perhaps have collapsed by the water having penetrated into the larger mother cell and pressed upon its wall.

In somewhat further developed rudimentary fruits (figs. 5, 6, 7) I have been equally unable, by preparation with needles, to set free the hitherto nearly central cell, overgrown by mycelium-filaments from beneath, or to detect any indication of it. Nor did anatomical examination with the aid of the knife furnish any satisfactory results for the formation of a clear notion of the further course of development of the fecundated ovicell*,

* If we are to regard the development of the fruit of the Fungi as a consequence of the cooperation of the two cells above described, and therefore to recognize in it a process analogous to the action of the pollen upon the embryo-sac, and characterizable as sexual, the oval pedunculated mother cell of the Fungus-fruit will correspond with the ovule of the Phanerogamia, as well as with the archegonium of the Cryptogamia, and is to be compared with a naked nucleus of the ovum, or the central cell of

as it appears to be, from analogy with *Cænogonium*. I could ascertain from it only that the outermost envelope of mycelium-filaments which forms over the central cell, and is comparable to the outer cortical layer of the apothecium of *Cænogonium*, becomes the general veil (*velum universale*) of the *Agaricus vaginatus*; further, that with the first development of the young fruit, which is soon of a globular form, the portion destined to form the peduncle of the developing fruit is produced by the increase and interlacing of the mycelium-filaments, especially those beneath the ovicell; and that the greatest accumulation of plasma occurs in the elongated cells which are here present; so that, probably, the most active formation of new cells takes place at first at the apex of this part of the peduncle (which is situated beneath the general veil), and soon afterwards a little below its apex.

Whether this cambial tissue is produced somewhat as in *Cænogonium*, from the nuclear cell which was contained in the ovicell, is a question which cannot yet be solved with certainty, although it will most probably be answered in the affirmative.

If this be the mode of development of the fruit in the Hymenomycetes, it will present the following differences from that of *Cænogonium*:—

In the apothecium of these Lichens (which, until it opens at the vertex and becomes expanded into a nearly flat disk bearing the hymenium, likewise forms a globular and completely closed body), the new generations produced in the fecundated central cell of the naked archegonium, which finally contain the spores as the last member of this series of cell-developments, are so arranged in the centre of the young fruit that all the spore-tubes lie in a radial direction.

Each of these numerous tubes produced from the fecundated germ-cell of the Lichen becomes united at its base (hitherto

the archegonium, which, even in the Algæ, generally occurs without an envelope. Hence this primitive mother cell of the Fungus-fruit, if we do not apply to it the general denomination of "ovicell," must be named the "archegonium," or perhaps, to distinguish it from that concealed in a simple stratum of cells, the "naked archegonium," as I have already explained (Bot. Untersuchungen, p. 91).

To give the name of "oogonium" to this organ on account of its want of an envelope, is just as unnecessary, and therefore unscientific, as to name the naked nucleus differently from that with one envelope, and this, again, differently from that with several coats. Who would now approve, if some one were to give different names to the simple scale-like leaf of the mosses, and to the linear grass-leaf, or the simple pedunculated leaf of a myrtle, and, again, a different name to the latter and to the composite leaf of the Leguminosæ, &c.

peripherally situated) with the tissue of the parent plant, in the same way as the fecundated germ-cell of the leafy Cryptogamia, amongst which it is especially comparable to that of the Mosses, growing by its inferior extremity into the tissue of the parent plant which conveys the nutritive fluid, and becoming more or less intimately amalgamated therewith (*l. c.* p. 92. vi. 2 c & 3, p. 94. vii. 5 & 8). By the subsequent opening and expansion of the young rudiment of the fruit, the apices of the spore-tubes and paraphyses, which previously lay together in its centre, become its extreme uppermost surface (p. 91. v. 5, 6, 9).

If I am not greatly mistaken, this condition is reproduced in the most correspondent manner in the fruits of the Liverworts which are furnished with a central column; at least, in these, up to the opening of the fruit, the elaters, which may be compared organologically with the paraphyses, are attached by their extremities to the columella (where this is present), and this may be compared with the medullary layer of the apothecium. (*Flora Columb.* xx. 23.)

According to my observations (which are certainly still imperfect) on the Discomycetes (*Peziza*, *Helvella*), similar conditions occur in these also; and there is no ground for supposing that the development of the Pyrenomycetes takes place in a very different manner, as the folds and chambers occurring in them may be explained just as simply by processes and excrescences of the inner surface of the fruit (which is simple in its earliest stages) as the separated compartments (*receptacula*) by the circumstance that the first generations of the fecundated germ-cells do not remain in close proximity, but are forced apart by the development of the medullary layer, and become isolated towards the surface of the fruit, after which each of them acquires an orifice on the peripheral side for the spore-tubes produced in it in the interim, in exactly the same way as the (in this sense) unilocular fruit of the Lichens.

Whether, and how far, a different condition occurs in the Hymenomycetes, remains to be decided by future investigations.

From my observations, I conceive the production of the pileus in the Hymenomycetes to take place in the same way as the isolation of the chambers of the Pyrenomycetes, namely, that the youngest generations of the fecundated germ-cell, which at first form a layer upon the peduncle developing itself beneath this, are forced asunder, penetrated, and overgrown by it, so that the cambial hymenium surrounds the apex of the peduncle in a circular form beneath the tissue of the pileus which grows over it, and from this grows downwards in various forms.

The most significant and important difference in the development of the hymenium of the Fungi, which is even indicated in

the distinction between asco- and basidiospores, and, in my opinion, increases the difficulty of understanding the development of the latter, consists in the fact that the spores of the Lichens and Ascomycetes are produced in a simple regular sequence of endogenous cell-development from the one fecundated ovicell, and only the last generation of the spore mother cells is slightly produced *downwards* in a peduncular form, becoming united with the subjacent tissue in the Basidiomycetes; on the contrary, a sprouting of the cambial hymenium-cells, which multiply and regenerate themselves for the development of the spores, takes place at a more or less early period of development. By this means, as also by the amalgamation of these superiorly elongated and branched hymenial cells of the Basidiomycetes with the neighbouring tissue of the pileus, the limits of the two tissues (of the pileus and hymenium) are more difficult to recognize than in most of the Ascomycetes.

EXPLANATION OF THE FIGURES.

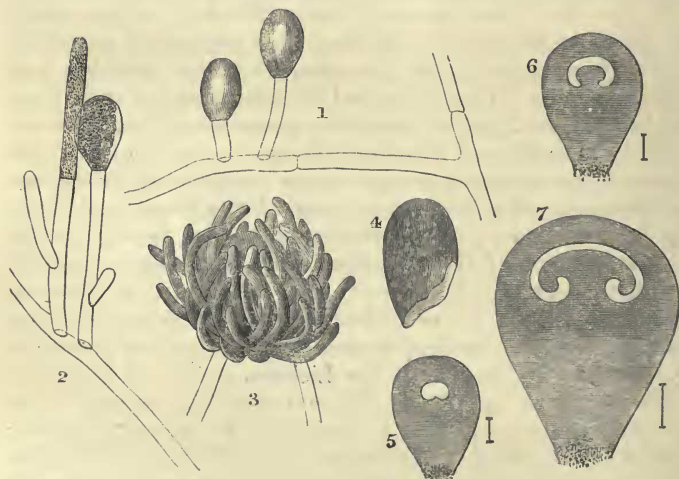


Fig. 1. Two naked archegonia of *Agaricus vaginatus*, Bull.

Fig. 2. A similar archegonium, and near it a cylindrical branch-cell amalgamated with it at the point of contact.

Fig. 3. A young fruit-rudiment, in the middle of which a large cell is to be seen.

Fig. 4. The large cell set free.

Fig. 5. Longitudinal section of an older fruit-rudiment, already covered by the cortical layer above this central cell.

Figs. 6 & 7. Two other young but more developed fruit-rudiments.